A REVIEW OF FACTORS INFLUENCING THE DISTRIBUTION OF SPIDERS WITH SPECIAL REFERENCE TO BRITAIN

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Duffey, E. 1993 11 11: A review of factors influencing the distribution of spiders with special reference to Britain. *Memoirs of the Queensland Museum* 33(2): 497-502. Brisbane. ISSN 0079-8835.

Available data on factors influencing spider distribution are synthesized using mainly British and other European information. The importance of landscape history is stressed, in fragmenting ancient natural habitats and creating new ones. It is postulated that this has reduced the number of specialists and allowed a range expansion of pioneer and euryoecious species. A tentative classification of life strategies is proposed. Habitat diversity and microspatial distribution are discussed with examples. □*Spiders, habitat preferences, geographic distribution, life strategies.*

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Many attempts have been made to categorise the habitats of spiders according to their preferences for dampness, dryness, shade, light, warm or cool temperatures. In addition, increasing knowledge derived from extensive collections made during the last 50 years in Britain and the rest of Europe have made it possible to draw distribution maps (Locket *et al.*, 1974; Ransy and Baert, 1985, 1987a, 1987b; Janssen and Baert, 1987; Ransy *et al.*, 1990; Alderweireldt and Maelfait, 1990; Canard, 1990), even though their incompleteness is acknowledged. The distribution of some species shows a clear influence of latitude and longitude, with north-south or east-west trends, or an association with major habitat formations. This paper discusses some factors which influence spider distribution, such as landscape history and geographic range, habitat preferences, adaptation to man-made biotopes and small-scale environmental differences, with the object of categorising the occurrence of species according to life strategy.

Islands of modest size such as Britain are poorer in species than adjacent continental areas. For example, the spider fauna of Belgium, a near neighbour, which is only 1/8th the size of Britain and has 75km of coastline compared with Britain's 19 000 km, and a lower landscape diversity, has almost as many recorded species (600) (Keckenbosch *et al.*, 1977) as Britain's 622 (Roberts, 1985-87).

Habitat labels based only on local information may be unsatisfactory, since (in Britain and the rest of Europe) we know that (a) some widespread species are found in different habitats according to where they occur in their geographic range; (b) within a restricted area some species are found only, or mainly, in 2 very different habitats, for example sand-dunes and marshes; (c) some species are so widespread that they are difficult to characterise in terms of habitat preferences; (d) species confined to only one specialised habitat are generally few in number and often rare. Examples are presented in this paper.

Nomenclature follows Roberts (1985-87) for spiders and Anon. (1964-80) for plants.

LANDSCAPE HISTORY AND PATTERN OF SPIDER DISTRIBUTION

Britain was largely forested before human settlement but forests are now much modified scattered remnants. This extensive environmental change will have favoured some species and disadvantaged others. For example, when the surviving rare species associated with major formations in Britain are listed (Table 1) most are recorded for coastal systems which–apart from the more limited mountain tops–are the least modified components of the present-day landscape. Species which are regarded as 'characteristic' of major habitat formations (Ratcliffe, 1977) (Table 2) may also be identified. The high numbers recorded for grassland, dry heaths and coasts probably reflect a great expansion of range by open-ground species after forest clearance.

The extent of habitat modification and disturbance is difficult to quantify because the type and intensity of change varies from place to place. In the case of wetlands, however, there is a common factor in that alteration to the water table has a greater impact on the fauna than other uses made

TABLE 1. Numbers of British spider species in the IUCN categories Endangered, Vulnerable and Rare, assigned to major habitats (compiled by P. Merrett in Bratton, 1991).

Coast- dune, shingle, saltmarsh, cliff	24
Dry lowland heaths	14
Fens-mesotrophic to eutrophic	12
Deciduous woodlands in lowlands	10
Caledonian (ancient) pine forest, Scotland	5
Grasslands-acidipholous to calcicolus	7
Wet heath/bog—oligotrophic	7
Open moorland, uplands and mountains	4

of these areas by man. In 1969 11 fens in East Anglia were surveyed by a group of arachnologists hand-collecting for a total of 10 hours per site. Each hourly collection was kept separate. The similarity between the faunas of the 11 fens in terms of abundance of each species present was assessed using Mountford's Index of Similarity (Mountford, 1962). Three groupings were derived, of which 2 were more similar than either was to the third group. The 8 fens in groups 1 and 2 had survived with little change to their water regimes at that time, while the third group had suffered falling water tables and hence vegetation changes (Duffey, 1974). The mean numbers of species for groups 1 and 2 were 53.2 and 50.0, respectively, and 34.6 species for group 3. Most of the rarer and more specialised fen species (*Marpissa radiata* (Grube, 1859); *Hygrolycosa rubrofasciata* (Ohlert, 1865); *Neon valentulus* Falconer, 1912; *Carorita paludosus* Duffey, 1971; *Centromerus incultus* Falconer, 1915; *Maso gallicus* Simon, 1894) were recorded in groups 1 and 2.

HABITAT VERSATILITY IN SPIDERS

The ability of many spiders to live successfully in a range of different environments has been little studied. The best known examples are pioneer species that are good aeronauts and the first to colonise newly created habitats. Meijer (1977) discusses this for Dutch polders, and Duffey (1978) for croplands and grasslands. Not all aeronauts behave in this way. *Erigone arctica* (White, 1852) and *E. longipalpis* (Sundevall, 1830) are often abundant on coastal driftlines and saltmarshes but are rare inland. The former is found on mountainsides in Sweden (the late A. Holm, pers. comm.) and both have been recorded on inland saline areas as well as in sewage works.

TABLE 2. Numbers of British spider species assessed as characteristic of various major habitats (compiled by P. Merrett in Ratcliffe, 1977)

Grasslands	74
Dry lowland heaths	63
Coastal formations	53
Deciduous woodlands	34
Fens	31
Wet heath/bog	21
Open moorland	17
Caledonian pine forest	14

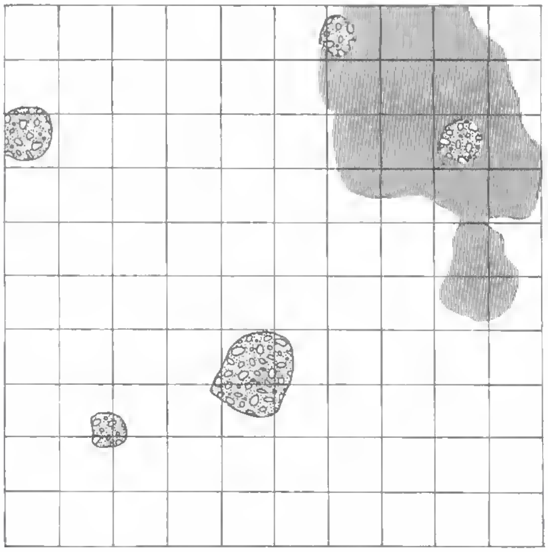
This provides evidence that they disperse over long distances but survive in only a few places.

Agricultural land has been colonised by species whose natural habitats are sand-dunes and stony open ground, for example *Troxochrus scabriculus* (Westring, 1851) and *Milleriana inerrans* (O.P.-Cambridge, 1884). *Porrhomma convexum* (Westring, 1861) is also frequent on cultivated land but elsewhere occurs in caves, mines, culverts (Locket and Millidge, 1953), and under stones by stream and lake shores (K. Thaler, pers. comm. and Duffey, unpublished).

The stone-filled filter beds of sewage works attract another cave species, *Lessertia dentichelis* (Simon, 1884), together with *Leptorhoptrum robustum* (Westring, 1851), whose natural habitat is freshwater marshes and wet meadows, and also *E. longipalpis* and *P. convexum*. The environment of filter-beds is completely artificial and uniform with stable temperature and high humidity, forming a 'super habitat' in which few species occur but in much higher numbers than found in nature.

The ability of some species to live successfully in two contrasting habitats was first noted by Bristowe (1939) and described as 'diplostenoecism' by Duffey (1974) and 'doppeltes ökologisches Vorkommen' by Schaefer and Tischler (1983). The best-known examples are those species found on coastal dunes and also in marshes–*Synageles venator* (Lucas, 1836), *Tibellus maritimus* (Menge, 1875), *Clubiona juvenis* Simon, 1878, *Hypomma bituberculatum* (Wider, 1834) and *Thanatus striatus* C.L. Koch, 1845. The last is also found in dry grasslands. *Sitticus rupicola* (C.L. Koch, 1837) is widespread on stony mountainsides in central Europe (Prószynski, 1978) but in England occurs only on coastal shingle banks.

Competitive relationships may also influence choice of habitat and hence distribution. *Zelotes electus* (C.L. Koch, 1834) is the characteristic species of this genus on coastal sand-dunes in



FIGS 1A-C. Distribution of spiders on 2.5x2.5m plot divided into 25x25cm quadrats on a Danish heathland.
1A. Vegetation map: Blank space, heather; lined shading, grass tussocks; cobbled, mosses, lichens and small stones.

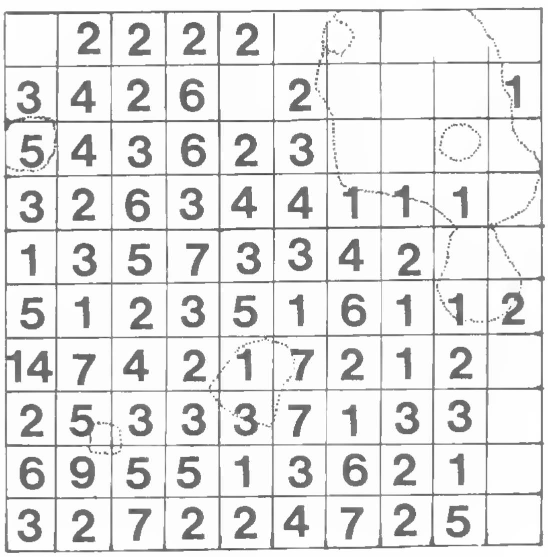


FIG. 1B. *Trichopterna cito*. A small web-spinning linyphiid almost confined to open ground with short, sparse vegetation; not a known active aeronaut nor a pioneer (Table 3) but a Narrow Specialist. Spread of heather eliminates it.

Britain whereas *Z. pusillus* (C.L. Koch, 1833) is associated with inland heaths, dry grasslands and open, stony ground. However, *Z. electus* was found (Anon., 1979) to extend only as far north as south-east Scotland and at higher latitudes was replaced on the coastal dunes by *Z. pusillus*.

All these species can adapt to different environmental conditions and emphasise the need to study habitat selection throughout the whole geographic range of a species before its distribution status can be understood.

EFFECTS OF HABITAT FRAGMENTATION

Several distribution maps in Locket *et al.* (1974) show widely scattered records for certain species which may indicate a decline from a former continuous distribution.

Lepthyphantes midas Simon, 1884 is an ancient forest specialist and is associated with loose bark and dead timber or birds' nests made of twigs. It is only known from 4 scattered sites in Britain where ancient forest survives. Similarly, wetlands have suffered serious losses, including the Fen Basin, East Anglia, which was progressively drained from Roman times and lost the remaining large areas of marsh in the mid-19th century. The local lycosid *Hygrolycosa rubrofasciata* (Ohlert, 1865) survives in the two remaining fenland areas and also in numerous small fen relicts around the

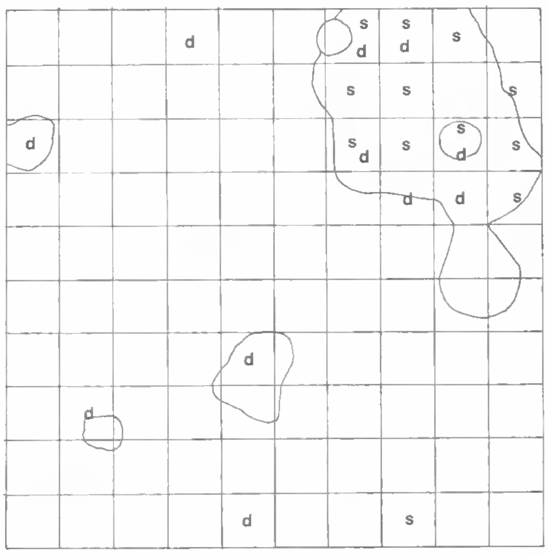


FIG. 1C. Other species preferred cover of heather plant or grass tussocks, e.g. *Scotina gracilipes* (Blackwall, 1859) (s) and *Dipoena prona* (Menge, 1868) (d). Each record refers to a catch of 1-5 individuals.

TABLE 3. Classification of life strategies and adaptability to environmental diversity based on British spiders.

PIONEER SPECIES
Active aeronauts which disperse freely, exploiting newly created open ground where competition is low. Widely distributed in temporary or changing habitats such as agricultural cropland, gardens, urban areas, leys and other types of disturbed ground or vegetation.
GENERALISTS
Common species with a capacity to adapt to a wide range of semi-natural habitats and permanent artefacts in the man-made environment. May be difficult to assign to a particular habitat.
BROAD SPECIALISTS
A. Widespread, euryoecious, or 'characteristic' species (Table 2) associated with major habitats such as deciduous woodland, marshes, heaths or ancient grassland, but may be found in many different variants of the chosen major formations.
B. Diplostenoecious species, mostly widespread and associated with 2 different habitats but usually more common in one than the other. Occasionally much more abundant in man- made habitats than in the natural environment. This grouping grades into species successful in 3 or more different environments.
NARROW SPECIALISTS
Stenoecious species which seem confined to clearly defined habitat. Includes rare species in low numbers and others which may be locally abundant, although confined to a restricted area because the habitat is scarce.

margins of the Fen Basin. Are these relicts of a former more extensive distribution?

Lowland heathland has also suffered severe losses, having been reduced to many small fragments by agricultural reclamation with a consequent loss of biodiversity (Webb, 1990). *Eresus niger* (Petagna, 1787) was formerly more widespread in heaths in southern England but is now known from only one locality where the population is small.

In contrast, some species are able to live in a range of different habitats, and thus overcome the problem of fragmentation. If this characteristic is also combined with active aeronautic dispersal, the chances of finding isolated suitable environments will be further enhanced. For example, *Pardosa palustris* (L., 1758) is the most active aeronaut of the common lycosids found in Britain and northern Europe (Richter, 1970). Few have been recorded in a wide variety of habitats, including marshes, grasslands, heathlands, and agricultural crops, but occasionally is found to be dominant, as in moist hay meadows in river valleys and on some sand-dunes. In a survey of dune systems in Scotland (Anon., 1979) it was the most abundant lycosid, although it was not recorded on all the dune areas which were studied. It seems that the active aeronautic behaviour of *P. palustris* enables it to move about freely and its ability to exploit many different habitats gives it a high ranking as an opportunist. Kessler (1973) also showed that *P. palustris* is able to produce more eggs per unit of body size under field conditions than 7 other *Pardosa* species. This may be an advantage when colonising new areas.

Adaptability to environmental diversity varies from species to species, so that a gradient exists from those which are very widespread (usually many species) to those which appear to be confined to a specialised habitat (relatively few species). The different components of this gradient are outlined in Table 3, and modified from Duffey (1975a).

HABITAT DIVERSITY AND MICROSPATIAL DISTRIBUTION

The structure of the vegetation, the litter layer and physical features of the environment have a strong influence on spider distribution and species composition (Duffey, 1962, 1968, 1974; Edwards *et al.*, 1975; Uetz, 1991). There is evidence that all species, however widespread, are influenced in some way by habitat structure. This was shown by comparing the fauna in different quadrats of a simple vegetation type on a Danish heathland (Duffey, 1974). Fig. 1 shows the differences in species and numbers of spiders between 100 25x25cm quadrats in a block measuring 250x250cm. The vegetation consisted of a heather plant (*Calluna vulgaris* (L.) Hull, 1808) in one corner of the block, and a few scattered grass tussocks of *Deschampsia flexuosa* ((L.) Trin., 1836), while most of the area was covered with mosses, lichens and small stones. The species in Fig. 1 occurred in clearly defined microhabitats. *Trichopterna cito* (O.P.-Cambridge, 1872), which was widespread in the open ground of moss and lichen, avoided the heather, and was also absent from 4 quadrats on the right-hand side of the sampling area which had been trampled. Similar results are reported by Jocqué (1973), who studied the fauna of different types of woodland litter layers in Belgium. On a heathland ranging from dry to wet areas, Snazell (1982) sampled the spider fauna by pitfall trapping at 154 random points over 12 months. By Principal Components Analysis on the 45 most numerous species he was able to show a wide gradation from specialised to broad habitat preferences, which conform well with the categories in Table 2.

In an experiment in tall grassland in England, faunal changes were recorded in grass litter modified by trampling. Samples of grass litter enclosed in nylon-mesh bags (20x20x8cm) received 3 different treading treatments (5 treads/month, 10 treads/month and an undisturbed control series) (Duffey, 1975b). There were 25 replicates in each case. After 12 months the volume of the litter in the controls had fallen by 50 % due to natural decay, but those having had 10 treads/month had fallen by 81 %. Of the 10 most frequent species, 5 were eliminated by the treading after 12 months, and the total numbers of all species fell by 84 %. Of the 5 remaining species, 3 showed little response to the treading, their numbers falling only marginally. The higher level of treading in this experiment was very light compared with that on a public footpath in a popular area, but the effect on the litter fauna was quite dramatic.

CONCLUSIONS

The modification of the European landscape through many centuries has been the greatest influence determining the distribution of spider species. Natural and near-natural habitats are now rare, as are the specialist species associated with them. Today many species have adapted to man-made environments, whether permanent or temporary, and those preferring open-ground conditions have greatly expanded their range. A gradation of life strategies (or adaptability) from pioneer species to narrow specialists is proposed. Superimposed on these factors are the influences of major climatic zones and the microspatial variations in the abiotic environment. All these features should be considered when defining the distribution and habitat characteristics of a species, drawing on evidence from the whole geographic range.

ACKNOWLEDGEMENTS

My grateful thanks to Malcolm Mountford and David Spalding for statistical help with the Index of Similarity.

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